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THE UPWARD TRANSLOCATION OF FOODS IN WOODY PLANTS. I. TISSUES CONCERNED IN TRANSLOCATION

Otis F. Curtis

It seems to be very generally believed that in shrubs and trees there is storage of organic matter in the lower part of the trunk and in the roots, and that, as growth starts in the spring, this food becomes soluble and passes upward through the xylem to the developing shoots and leaves.

The fact that has been most commonly offered as proof of upward translocation through the xylem is that the xylem tissues of woody plants commonly contain quantities of organic storage products, particularly sugars and starches. It has been shown by Atkins (1916), Fischer (1891), and others that not only the living parenchyma cells but also the water-conducting cells proper, the tracheae and tracheids, contain appreciable quantities of soluble carbohydrates, and Atkins has found these to be present at all seasons of the year. The latter considers that sugars are commonly carried through the xylem. He even goes so far as to say that ". . . the transference of carbohydrates can no longer be regarded as an occasional and accessory function of the vessels, but is certainly a continual and principal function . . . ." It may well be, however, that there is no flow of solution through the xylem for any great distance, for a possible frequent interposition of living cells across the water-conducting tissues may prevent such a flow. Atkins himself clearly recognizes that water may flow across tissues containing a high solute content without carrying the solutes with it.

Experiments performed by Hartig (1858) are also commonly cited in texts as offering proof of upward translocation through the xylem. Hartig ringed a number of trees early in the summer and found early in the following spring that the starch stored below the ring had disappeared. He concluded that the storage products must have been translocated upward through the xylem. It might be, however, that the food stored below the ring was used locally for growth in diameter, or that it was translocated downward through the phloem and was used in root growth.

In order to determine more definitely whether the upward translocation of food takes place primarily through the phloem or through the xylem, the writer has conducted a series of experiments part of which are reported in this paper. Some of these experiments also throw light on the matter of food movement from roots or trunks to growing shoots. The discussion therefore naturally falls into two main parts: (1) When upward translocation of organic matter takes place, as it certainly must for at least short distances, does it take place through the water-conducting tissues, the xylem, or through the phloem? And (2) Is there normally an upward movement of this food from the roots and lower trunk to the growing shoot? The present discussion will deal with the former question; the second question will be discussed in a subsequent paper.

EFFECT OF RINGING ON GROWTH OF LEAFY AND DEFOLIATED SHOOTS.

Vigorous young shoots of *Philadelphus pubescens* Loisel. were treated on May 30 as indicated in table 1. In this as in subsequent tables those shoots having the same letter were fairly well matched as to size, vigor, and position on parent plant.

TABLE 1. *Philadelphus pubescens. Rings in new growth 15–20 cm. from tip. Stems measured from attachment to main stem. May 30 to June 8, 1918*

	1 Not Ringed. Leaves Remaining			2 Ringed 15–20 Cm. from Tip. Leaves Remaining			3 Not Ringed. Leaves Removed from Upper 15–20 Cm.			4 Ringed 15–20 Cm. from Tip. Leaves Above Ring Removed		
	Length in Cm. May 30	Length in Cm. June 8	Gain in Cm.	Length in Cm. May 30	Length in Cm. June 8	Gain in Cm.	Length in Cm. May 30	Length in Cm. June 8	Gain in Cm.	Length in Cm. May 30	Length in Cm. June 8	Gain in Cm.
a ...	52.5	81.5	28.5	61.0	79.0	18.0	40.0	69.0	29.0	58.5	58.5	0.0
b....	58.0	79.5	21.5	60.0	75.0	15.0	53.5	85.0	31.5	60.5	61.5	1.0
c....	49.5	85.0	35.5	78.0	Broken	–	40.5	66.0	25.5	63.5	81.5	18.0[1]
d....	54.0	90.0	45.0	61.0	67.0	6.0	64.0	92.5	28.5	55.0	55.5	0.5
e....	59.0	99.0	40.0	59.0	67.0	8.0	60.0	80.5	20.5	58.0	80.0	22.0[1]
Average gain			34.1			11.75			27.0			0.5

The measurements of June 8 show very clearly that ringing has in some way checked the growth of the shoots. The simplest explanation appears to be that the food necessary for shoot formation passes upward through the phloem and not through the xylem tissues. The few leaves present above the ring (group 2) are able to synthesize sufficient food to allow for some growth. In two shoots of group 4 a narrow strip of phloem was left by accident, and this has served to transfer sufficient food to allow for considerable growth. Two or three small leaves unfolded at the apex of the stems of group 4, but these were too small to carry on much photosynthesis, so growth continued very slowly for several weeks until other leaves had developed.

The same experiment was repeated with Philadelphus in the spring of 1919, except that in this case, instead of making the ring in the upper part of the new growth, the ringing was done on the wood of the previous year just below the bases of the young shoots. As the stems had been cut back when dormant, this left the new shoots at the apex of the stem. In each case, whether the leaves were or were not removed, one pair of leaves enclosing the growing tip was removed. The measurements are recorded in table 2, and a photograph of those shoots lettered *g* is shown in figure 1.

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[1] Not included in average. A strip of phloem was left on about ¼ of the circumference. The twig was bent at an angle at this point.

TABLE 2. *Philadelphus pubescens. Paired shoots measured from attachment to old stem. Rings made on old wood just below attachment of young shoots. May and June, 1919*

	1 Not Ringed. Leaves Remaining			2 Ringed. Leaves Remaining			3 Not Ringed. Leaves Removed			4 Ringed. Leaves Removed		
	Length in Cm. May 30	Length in Cm. June 4	Gain in Cm.	Length in Cm. May 30	Length in Cm. June 4	Gain in Cm.	Length in Mm. May 30	Length in Mm. June 4	Gain in Mm.	Length in Mm. May 30	Length in Mm. June 4	Gain in Mm.
	19.0	35.5	17.5	16.0	27.5	11.5	4.0	10.5	6.5	14.0	15.5	1.5
a	18.5	33.5	15.0	14.5	26.5	12.0	16.0	27.5	11.5	12.5	14.0	1.5
	17.0	30.5	13.5	15.0	27.5	12.5	13.0	20.5	7.5	19.0	21.5	2.5
b	17.5	31.5	14.0	18.5	31.5	13.0	14.5	22.5	8.0	16.5	17.5	1.0
	25.5	46.5	21.0	21.0	29.0	8.0	19.5	26.0	7.5	15.0	16.0	1.0
c	13.0	30.0	17.0	23.0	35.0	12.0	18.0	22.5	4.5	19.0	20.5	1.5
	23.0	40.5	17.5	20.5	35.0	14.5	17.0	25.0	8.0	16.5	15.5	2.0
d	23.0	42.0	19.0	24.0	38.0	14.0	15.0	24.0	9.0	20.0	21.5	1.5
	12.5	28.0	15.5	24.0	39.5	15.5	16.0	25.0	9.0	15.5	17.0	1.5
e	18.5	35.0	16.5	24.5	40.0	15.5	23.0	35.5	12.5	15.5	17.0	1.5
	20.0	36.5	16.5	21.5	33.5	12.0	16.5	19.0	2.5	20.0	22.5	2.5
f	20.0	38.5	18.5	21.5	35.0	13.5	24.5	28.0	3.5	20.5	22.5	2.0
	15.5	29.0	13.5	24.5	38.0	13.5	24.5	30.0	5.5	28.5	30.0	1.5
g	20.5	34.5	14.0	27.5	41.5	14.0	21.5	27.5	6.0	26.5	27.5	1.0
Ave.			16.36			12.96			7.96			1.61
	Length in Mm. June 3	Length in Mm. June 6	Gain in Mm.	Length in Mm. June 3	Length in Mm. June 6	Gain in Mm.	Length in Mm. June 3	Length in Mm. June 6	Gain in Mm.	Length in Mm. June 3	Length in Mm, June 6	Gain in Mm.
	32.0	39.5	7.5	38.0	45.0	7.0	45.0	47.5	2.5	24.0	25.5	1.5
h	27.0	35.0	8.0	33.0	40.0	7.0	43.0	46.5	3.5	38.0	38.5	0.5
	28.0	36.0	8.0	41.5	49.0	7.5	36.5	40.0	3.5	36.0	37.5	1.5
i	43.0	53.5	10.5	38.0	45.5	7.5	26.5	29.5	3.0	25.5	27.5	2.0
	42.5	54.0	11.5	42.5	51.0	8.5	44.5	48.0	3.5	35.0	36.5	1.5
k	42.5	52.5	10.0	31.5	38.5	7.0	37.0	40.0	3.0	30.5	32.0	1.5
	42.5	52.5	10.0	40.5	47.0	6.5	46.0	50.5	4.0	28.5	30.0	1.5
l	43.5	53.0	9.5	42.0	48.0	6.0	41.5	46.5	5.0	28.5	30.0	1.5
Ave.			9.38			7.13			3.56			1.44

The results of this second experiment are similar to those of the previous one. It is noticeable, however, that the ringed shoots with leaves (group 2) in this experiment show greater growth than shoots without leaves and not ringed (group 3), while in the previous experiment the reverse was true. In the experiment of 1918 only a third to a half of the new shoot was above the ring or was leafless, while in that of 1919 the whole of each new shoot was above the ring. It seems very probable that the older leaves of the new shoot manufacture a large part of the food used in terminal growth after the shoot is well started.

A similar experiment was tried with a tree of Northern Spy apple. This was started near the end of the growing season, which fact accounts for the small amount of growth obtained. All growth on this tree was practically completed by June 30, whereas with most of the other trees of the orchard it was nearly completed on June 11.[2]

[2] The writer is much indebted to Prof. W. H. Chandler, of the department of pomology, who very kindly offered him the trees of the department orchard for experimentation,and to Prof. E. C. Auchter, now of the Maryland Agricultural Experiment Station, who assisted in these experiments with the apple.

TABLE 3. *Pyrus malus (Northern Spy). Rings made 15 cm. from tip in present year's growth. Measurements from last bud scale scar to tip. June 11 to June 30, 1918. All growth was practically completed by June 30*

	1 Not Ringed. Leaves Remaining			2 Ringed. Leaves Remaining			3 Not Ringed. Leaves Removed			4 Ringed. Leaves Removed		
	Length in Cm. June 11	Length in Cm. June 30	Gain in Cm.	Length in Cm. June 11	Length in Cm. June 30	Gain in Cm.	Length in Cm. June 11	Length in Cm. June 30	Gain in Cm.	Length in Cm. June 11	Length in Cm. June 30	Gain in Cm.
a....	26.2	30.5	4.3	24.5	30.0	5.5	23.0	25.5	2.5	23.3	23.0	0.0
b....	26.0	29.5	3.5	17.5	22.0	4.5	24.8	28.0	3.2	21.5	21.0	0.0
c....	26.5	32.5	6.0	23.5	Broken	—	19.5	23.5	4.5	24.5	25.0	0.5
d....	25.0	29.5	4.5	20.0	24.5	4.5	23.3	28.0	4.7	22.5	23.0	0.5
e....	20.7	22.0	1.3	26.5	32.5	6.0	24.0	24.5	0.5	22.4	24.5	0.1
f....	25.7	33.0	7.3	23.0	29.0	6.0	22.2	27.0	4.8	24.6	25.0	0.4
Ave.			4.48			5.3			3.37			0.25

It is to be noted in this case that the ringed twigs which retained their leaves made a growth greater than did similar twigs not ringed. This difference is not striking, but in only one pair (*f*) is there greater growth of the stem not ringed. It would seem that food manufactured by the leaves was beginning to be removed downward and that the ring had checked this removal, thus increasing the supply for continued apical growth. The final cessation of growth of all twigs is evidently brought about by conditions correlated with the rest period which will not be discussed here. The almost complete lack of growth of the ringed twigs that had been deprived of their leaves coincides with the similar results obtained with Philadelphus. Evidently ringing has entirely prevented the upward translocation of some material or materials necessary for growth.

Further experiments of the same nature were tried with *Ligustrum ovalifolium* Hassk. Sone of the results obtained are presented in table 4. Other experiments showed results practically identical with these, so it is hardly necessary to present all of them.

From these experiments it seems very clear that the ringing has prevented the upward movement of some substance or substances necessary for growth. When leaves are present above a ring, these produce enough of this substance to allow for continued growth. Evidently the check in growth is not due to lack of water resulting from injury to the xylem, for those stems that were ringed but retained their leaves always made fair growth, which occasionally even exceeded that of the checks. Under certain conditions, however, ringing does seem to be followed by withering of the parts above the ring. This occurs especially when the ring is fairly near the young tip but only when no leaves are left above the ring. Hanstein (1860) obtained similar results and concluded that lack of water cannot be the cause of the withering, for when leaves remain above the ring, certainly more water is necessary but growth continues, while the shorter the part above the ring the less water it will need but the quicker is its death, even in a moist atmosphere.

TABLE 4. *Ligustrum ovalifolium. Bushes killed nearly to the ground by the cold winter. Experiments with the strong young shoots, June, 1918. All ring wounds had healed over by August 1. Some of no. 4, however, were not perfectly healed*

Hedge No. 1	1 Not Ringed. Leaves Remaining		2 Ringed 20–24 Cm. from Top. Leaves Remaining		3 Not Ringed. Leaves Removed for a Distance of 20–24 Cm. from Top		4 Ringed 20–24 Cm. from Top. Leaves Above Ring Removed	
	Growth in Cm. June 18–July 3	Growth in Cm. July 3–Aug. 1	Growth in Cm. June 18–July 3	Growth in Cm. July 3–Aug. 1	Growth in Cm. June 18–July 3	Growth in Cm. July 3–Aug. 1	Growth in Cm. June 18–July 3	Growth in Cm. July 3–Aug. 1
a.......	15.0	33.5	15.0	23.5	7.5	26.5	0.5	14.5
b.......	15.0	32.5	16.0	29.5	9.5	34.5	1.0	12.0
c.......	13.8	31.5	12.3	20.5	8.0	28.0	1.0	10.0
d.......	10.5	27.5	14.5	27.5	7.5	21.0	1.0	15.5
e.......	9.0	20.0	15.0	20.0	5.5	16.0	0.5	12.0
f.......	15.0	25.0	15.5	broken	6.5	10.5	0.5	9.5
g.......	17.0	32.5	14.0	27.0			0.5	13.0
Ave.....	13.61	28.93	14.61	24.67	7.41	22.75	0.71	12.36
Hedge No. 2	Growth in Cm. June 19–July 3	Growth in Cm. July 3–Aug. 1	Growth in Cm. June 19–July 3	Growth in Cm. July 3–Aug. 1	Growth in Cm. June 19–July 3	Growth in Cm. July 3–Aug. 1	Growth in Cm. June 19–July 3	Growth in Cm. July 3–Aug. 1
h.......	15.0	30.0	15.0	13.0	3.5	25.0	0.4	16.1
i.......	11.0	18.5	10.0	11.5	5.5	19.5	0.5	1.0
j.......	13.5	17.0	11.5	12.0	8.0	15.0	0.0	13.0
k.......	12.5	26.0	9.0	broken	7.0	12.0	0.0	5.5
l.......	10.0	29.5	9.5	9.0	6.5	18.0	0.0	2.2
m......	12.5	22.5	8.5	3.0	4.0	broken	0.5	5.0
Ave.....	12.49	22.41	10.58	9.7	5.75	17.9	0.23	7.11

Hanstein explained this lack of growth and the death above a ring when the leaves are removed on the grounds that "newly assimilated sap" is necessary. He accepted Hartig's idea that the stored food, particularly carbohydrates, readily moves upward through the xylem, but believed that this newly assimilated food moves in the phloem only. When leaves remain above a ring, they supply this essential food. Furthermore, Hanstein found that ringed willow cuttings placed in dry air showed a withering of the phloem above the ring while the presence of leaves prevented withering. He concluded that water cannot readily move from xylem to phloem and that the leaves aid in this transfer. According to his ideas, therefore, the leaves supply "newly assimilated sap "which is necessary for growth and can be carried through the phloem only, and they aid in transmitting the water to the phloem when the latter is separated from the roots by a ring.

If, however, all foods, including sugars, were translocated upward through the phloem only and not through the xylem, ringing would check further growth by withholding all necessary foods, and the withering might be due therefore not to the lack of any particular food, newly assimilated or otherwise, but to a deficiency of osmotically active substances, perhaps carbohydrates. Chandler (1914) has clearly demonstrated that, if tissues having different osmotic concentrations are organically connected, that tissue having the higher concentration will withdraw water from the other, causing the latter to wither. He demonstrated that leaves may withdraw water from fruits, or that a tomato plant having a high sugar content, if grafted to one with a lower sugar content, may withdraw water from the latter, causing it to wither.

In order to determine whether ringing and defoliation have any effect on the concentration of the sap, the freezing points of the sap from some of the stems of Philadelphus, previously described in table 2, were determined. The shoots were in pairs, as shown in figure 1, and for each determination both stems of the pair were used. As soon as possible after cutting the shoots, the leaves were removed and the stems were immediately cut into short pieces and placed in large test tubes which were then quickly plunged into a freezing mixture. After the tissues were thoroughly frozen they were ground in a mortar and the freezing point of the pulpy mass was determined. The material from each of numbers 1, 3, and 4 was extracted in 80 percent alcohol and this extract was hydrolyzed and analyzed for reducing sugars. The total sugar found, expressed as invert sugar, is recorded with the other

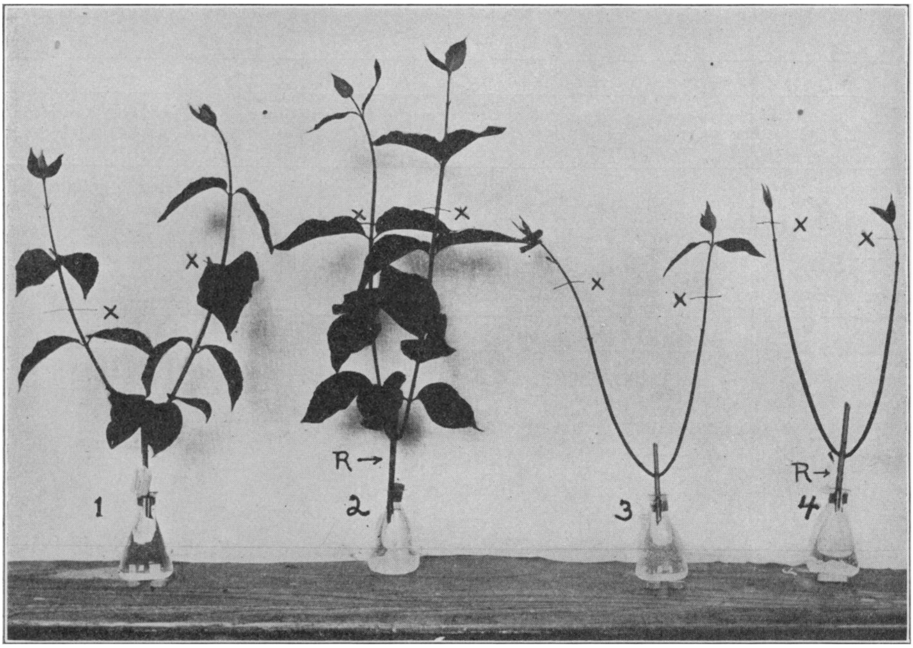

FIG. 1. Effects of ringing on leafy and defoliated shoots of Philadelphus.
1. Not ringed, leaves remaining.
2. Ringed, leaves remaining.
3. Not ringed, leaves removed.
4. Ringed, leaves removed.
Black strings tied at *x* indicate the original length of the shoots.

data in table 5. In table 6 are given the freezing point lowerings of the terminal pair as well as of the first pair of stems below the terminal pair. These were determined for the same series but on a different day.

TABLE 5. *Philadelphus pubescens. Effect of ringing and removal of leaves on growth osmotic concentration, and soluble sugar content of the stem*

		Length of Shoots in Cm. May 30	Length of Shoots in Cm. June 4	Gain in Cm. Length	Ave. Gain per Pair.	Freezing Point Depression Δ	Green Weight	Total Dry Weight	Mg. Invert Sugar per Gm. Green Weight	Mg. Invert Sugar per Gm. Dry Weight
1. Not ringed, leaves present	*a*	19.0	36.5	17.5			10.0			
		18.5	33.5	15.0	16.25	0.65°				
	d	23.0	40.5	17.5						
		23.0	42.0	19.0	18.75	0.69°	15.6	1.74	7.81	114.9
2. Ringed, leaves present	*a*	16.0	27.5	11.5						
		14.5	26.5	12.0	11.75	0.60°	8.9			
	d	20.5	35.0	14.5				—	—	—
		24.0	38.0	14.0	14.25	0.62°	12.0			
3. Not ringed, leaves removed	*a*	4.0	10.5	6.5						
		16.0	27.5	11.5	9.00	0.61°	4.7			
	d	17.0	25.0	8.0						
		15.0	24.0	9.0	8.50	0.61°	4.9	0.64	4.5	67.6
4. Ringed, leaves removed	*a*	14.0	15.5	1.5						
		12.5	14.0	1.5	1.50	0.455°	2.7			
	d	16.5	18.5	2.0						
		20.0	21.5	1.5	1.75	0.52°	6.4	0.445	2.6	52.2

TABLE 6. *Philadelphus pubescens. Effect of ringing and removal of leaves on osmotic concentration of the stem as compared with the concentration of lower shoots of the same stem*

		Total Gain for Each Pair of Shoots, May 30–June 4	Green Weights	Δ	Green Weight of First Shoots Below	Δ of First Shoots Below
1. Not ringed, leaves present	(*e*)	320	9.5	0.61	10.2	0.615
	(*f*)	350	12.9[3]	0.62	4.4	0.62
2. Ringed, leaves present	(*e*)	310	16.8	0.63	8.2[3]	0.675
	(*f*)	255	8.8	0.63	12.9	—
3. Not ringed, leaves removed	(*e*)	215	10.0	0.585	10.1[3]	0.59
	(*f*)	60	5.3	0.61	6.8[3]	0.57
4. Ringed, leaves removed	(*e*)	30	4.8	0.53	5.3	0.655
	(*f*)	45	6.3	0.59	—	0.66

The cryoscopic data thus far obtained are not sufficiently extensive to warrant a detailed discussion, but they clearly show that the ringing of a defoliated shoot results in a distinct falling off of the osmotic concentration of that shoot. Whether the check in growth is due primarily to a lack of food necessary for energy or for building material, or to lack of water resulting from a deficiency of osmotically active substances, is not clear. From the available data it would seem, however, that the former is of first importance. In a number of instances it was found that the part above a ring would grow slightly, and later would wither completely when the competition for water became more severe. Table 6 indicates, that, as would be expected, the ringing not only decreases the concentration above the ring but also tends to increase that below.

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[3] These are single shoots, not pairs.

These few determinations cannot be fully relied upon for all details, but, assuming that they are approximately correct, it can be readily seen why the part above a ring cannot compete for water with other parts unless it retains its leaves. This therefore would explain the withering of ringed shoots that lack leaves, and shows that the leaves do not directly draw water to the phloem as suggested by Hanstein, but rather that they supply the phloem with osmotically active substances, thus indirectly enabling it to obtain its own water.

It might be stated in this connection that the writer has obtained considerable evidence that one important factor among several possible factors that may be concerned in the matter of polarity and inhibition is associated with a local distribution of foods and of osmotically active substances. The same substance, possibly sugar, may act in both rôles. It has been found, for instance, that the upper part of a rapidly growing shoot may have a concentration that would give a pressure over two atmospheres greater than the concentration in the middle or lower part of the same shoot. The "inhibition" of shoot growth at nodes below the terminal one may be due to a lack of sufficient food and to inability to compete successfully for water rather than to a backward flow of some "inhibitor." In fact, as was shown in a previous paper (Curtis, 1918), it is possible to reverse the polarity by placing the base of a shoot in a strong sucrose solution. The writer has found that other substances are even more efficient than sucrose in thus altering the polarity of a shoot. The check in growth following ringing cannot be due to retardation in removal of an "inhibitor" produced by the leaves, for, if leaves remain, the growth is greater than if they are removed.

THE TRANSLOCATION OF FOOD TO FRUITS

It has been recognized that at least part of the food carried to growing fruits probably moves through the phloem. Hanstein (1860) found that ringing below fruits, if no leaves were left above the ring, resulted in checking their further development. In order to determine the effect of ringing on the transfer of food to fruits, twelve fairly well matched pairs of young Wealthy apples were selected. The leaves from the stems close to the fruit were removed, and the stem of one of each pair was ringed so that no leaves were above the ring. The greatest length and the greatest diameter of each fruit were taken. The same thing was done with three pairs of Rhode

TABLE 7. *Pyrus malus. Effect of ringing on movement of food to fruit. Leaves removed above ring and to same extent on those not ringed except in No. 3 (o) in which case leaves were left above ring*

		Aug. 6, 1918		Sept. 25, 1918							
		Average of Length and Diameter, Mm.	Approximate Volume, Cc.	Average of Length and Diameter, Mm.	Approximate Volume, Cc.	Gain in Approximate Volume, Cc.	Green Weight, Gm.	Dry Weight, Gm.	Relative Gain in Approximate Volume. Check as Unity	Relative Green Weight. Check as Unity	Relative Dry Weight. Check as Unity
1. Wealthy not ringed........	*c*	45	47.66	63	130.77	83.11	113.8	16.74			
	d	43	41.58	45.5	49.26	7.68	63.0	7.82			
	e	40.5	34.74	52.0	83.54	48.80	71.2	10.30			
	f	45.5	49.26	57	96.86	47.60	88.6	11.80			
	i	41	36.05	56.5	94.33	58.28	85.9	11.74			
	j	44	44.55	54.5	84.66	40.11	72.1	10.00			
	Ave.	43.17	42.31	54.75	89.90	47.60	82.43	11.40		1.00	1.00
Wealthy ringed...........	*b*	41.5	37.38	42.5	40.15	2.77	36.9	4.80			
	d	46.5	52.58	46	50.91	−1.68	47.8	6.66			
	f	41.5	37.38	42	38.75	1.37	38.0	5.05			
	g	41.5	37.38	40.5	34.74	−2.64	33.6	4.98			
	h	37.75	28.14	38.5	29.90	1.76	27.7	3.70			
	i	40.75	35.39	41.5	37.38	1.99	38.0	5.03			
	k	45.5	49.26	46.5	52.58	3.32	47.1	5.48			
	l	41.5	37.38	42	38.75	1.37	39.5	5.06			
	Ave.	42.06	39.36	42.44	40.40	1.03	38.58	5.10	0.02	0.47	0.45
2. Rhode Island Greening not ringed..................	*m*	48.5	59.67	63	130.77	71.10	121.7	18.43			
	n	48.0	57.84	55.5	89.41	31.57	93.4	13.90			
	o	52.0	83.54	67	157.30	73.76	154.7	21.53			
	Ave.	49.5	67.02	61.8	125.83	58.81	123.3	17.95		1.00	1.00
Rhode Island Greening ringed	*m*	48	57.84	49.5	63.43	5.59	60.5	8.80			
	n	48	57.84	49	61.53	3.69	62.7	8.86			
	o	51	69.38	53	77.86	8.48	77.3	9.48			
	Ave.	49.0	61.69	50.5	67.61	5.92	66.83	9.05	0.10	0.54	0.50
3. Rhode Island Greening ringed with leaves..............	*o*	52.5	75.68	57	96.86	21.18	92.40	12.61	0.36	0.75	0.71

Island Greenings, and in addition two stems were left without removing the leaves above the ring. The fruit was gathered on September 25 at which time a number had fallen from the trees, which fact accounts for the missing apples. The average of the greatest length and the greatest diameter was taken as the diameter of a sphere and the volume of this sphere was calculated. The data are presented in table 7.

There seems to have been practically no increase in the volume of the apples on the ringed stems. The 2 percent recorded is possibly within the range of probable error. Whether there was a transfer of anything but water to the fruits cannot be definitely determined from the data available, but the fact that both the water content of the fruit from the ringed stem and the volume-dry weight ratio of the same fruit were greater than in the fruit from the stem that was not ringed, as well as greater than in samples taken at the time of ringing, would indicate that no appreciable amount of food had moved to the fruit. The water contents of the fruit from the ringed stem, of that from the unringed stem, and of that taken at the time of ringing were respectively 86.9 percent, 86.2 percent, and 85.0 percent, and the approximate volume-dry weight ratios were respectively 7.92, 7.89, and 7.05.

EFFECT OF RINGING DORMANT TWIGS IN THE SPRING

Dormant stems of various woody plants were ringed at different distances from the tip to determine whether food stored in the xylem would move longitudinally through the same tissues and to determine from how far

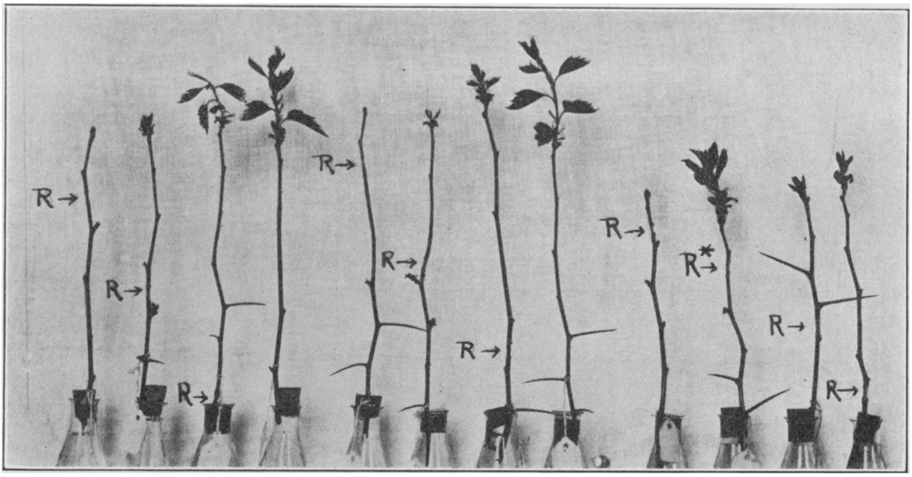

FIG. 2. Crataegus ringed, while dormant, at different distances from the tip. The place of ringing is indicated by *R*. In the stem marked *R** a narrow strip of phloem less than one fourth the circumference was left. Similar results were obtained when only one half of the xylem and one fourth of the phloem were left. (The unringed twig of the group at the right was omitted by the engraver. This twig showed a growth almost identical to that of *R*.*)

back the food supply was drawn. In all cases starch was present in the xylem at the time of ringing. Results obtained when twigs of Crataegus were ringed in this way are shown in table 8.

TABLE 8. *Crataegus sp. Ringed April 8. Measured May 8*

X. Check not ringed.
A. Ringed in 2nd internode from tip.
B. Ringed in 4th internode from tip.
C. Ringed at base of one-year-old wood, usually the 7th or 8th internode.
D. Ringed back on three- or four-year-old wood.

Those marked *z* had half the xylem cut away and three fourths of the phloem. One fourth of the phloem was left.

Lateral buds removed from all.

	X	*A*	*Az*	*B*	*Bz*	*C*	*D*
1.	20	0	—	0	—	16	16
2.	25	14	20	broken	—	16	20
3.	25	2	—	—	—	—	17
4.	25	3	—	8	—	9	—
5.	28	4	—	4	20	—	15
6.	25	6	27	4	—	—	20
7.	35	8	32	8	—	25	30
8.	30	3	—	broken	—	—	—
9.	20	—	—	6	30	20	—
10.	28	6	28	5	—	22	21
11.	27	broken	—	broken	—	—	—
12.	25	—	20	9	—	—	30
13.	30	6	9[4]	10	32	—	—
14.	25	9	10[4]	13	30	—	28
15.	28	7	9[4]	13	—	18	—
16.	30	12	8[4]	16	—	—	25
17.	30	—	30	9	—	10	20
Ave.	26.8	6.1	26.2	8.1	28.0	17.0	22.0

From these results it is apparent that material carried by the phloem is necessary for shoot growth. The check in growth cannot be due to any injury to the xylem, for if half the xylem is cut away and but a quarter of the phloem is left, growth is practically normal. This is shown in the columns *Az* and *Bz* of table 8 and in figure 2. Two possible explanations occur. Either the xylem carries no foods, neither carbohydrates nor nitrogenous material, or the xylem carries certain foods, perhaps carbohydrates, while the phloem carries some other substances, possibly nitrogenous, which may be necessary for growth. If the second alternative were true, the greater the amount of phloem above the ring the greater would be the supply of this substance which may act as a limiting factor. The following data, however (table 9), offer strong evidence that the carbohydrate supply is the limiting factor and that this cannot move upward through the xylem.

[4] These results are not included in the averages, for the wounds were not paraffined and the xylem had dried out checking the growth of the shoot.

TABLE 9. *Crataegus sp. April to May 18, 1919*

X. Check, not ringed.
A. Ringed at the second internode below the terminal bud.
B. Ringed at the fourth internode below the terminal bud.
C. Ringed at the seventh or eighth internode below the terminal bud.
All lateral buds were removed in each case.

No.	*X*		*A*		*B*		*C*	
	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves
1.......	65	5	0		0	dried	8	3
2.......	70	7	7	(green only	15	2	35	4
3.......	85	8	0		15	3	30	—
4.......	45	4	(*a*) 1 (*b*) 0	(green only)	10[6]	1	35	3
5.......	40	5	0	dried	20	(green only)	35	4
6.......	35	8	6	(green only)	15	(green only)	10	green
7.......	70	–	(*a*) 6 (*b*) 30[5]	(green only)	12	(green only)	20	—
8.......	(*a*) 55 (*b*) 50	5 5	0 60[5]	dried 5	0	dead	30	2
Ave.....	57.2	6.2	2.2	0	11.0	0.5	25.4	2.7

Starch tests:

X. Starch fairly abundant in primary xylem, pith, medullary rays, and outer cortex, both near the tip and near the base. In nos. 2, 3, 4, 7, 8*a*, and 8*b*, cambial growth was started and starch had largely disappeared from the outer part of the medullary rays.

A. No trace of starch above rings except in no. 5 which contained traces in the pith. Below rings just as in checks. Nos. 4, 6, and 7 tested for starch in region of ring showed none in upper part, traces in middle, similar to check in lower part.

B. No traces of starch above rings, except in nos. 1 and 8 which had evidently died early. Below rings just as in checks. Nos. 5, 6, and 7 tested for starch in region of ring showed none in upper part, while the lower part appeared about the same as just below the ring.[6]

C. No starch above the rings, except in no. 6 in which the terminal bud had been broken off and adventitious buds were just starting. In three cases there were slight traces in 2–3 pith cells. Below rings starch was fairly abundant as in the check stems.

In each case in which growth had ceased, the starch above the ring had disappeared. If something other than sugar were the limiting factor, one would expect that the starch could not be utilized, yet the shorter the piece above the ring the more rapid was the disappearance of the starch and the earlier the cessation of growth. In a few exceptions with Crataegus and Acer a very short piece above a ring sometimes died before all the starch had disappeared. In the checks, on the other hand, the starch had not all disappeared at the time the data of table 9 were taken. Later, however, as the shoot growth neared completion, starch disappeared from the checks also. It is evident that, when the stem is not ringed, a shoot does not first deplete the starch in its immediate neighborhood, but the starch for some distance is reduced rather uniformly.

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[5] In these twigs a narrow strip of phloem was left covering less than one fourth of the circumference.

[6] In no. 4 a narrow strip of phloem had healed over under the paraffin. Starch was fairly abundant in primary xylem, pith, and medullary rays. None in cortex. Below ring same as in checks.

TABLE 10. *Acer saccharum. Ringed April 7, 1919.*
Ringed in middle of first year's growth

	Growth in Mm. by May 11		Notes
	Ringed Branch	Corresponding Branch Not Ringed	
1...	10	55	*May 11*, nos. 1, 4, and 5 and their corresponding check twigs were cut and tested for starch. *Above ring:* In each case no trace of starch present above the ring; neither directly under the terminal node, in the middle internode, nor in the basal internode. *Below ring:* Starch present in each case in the primary xylem and in the medullary rays in all parts below the rings. *Within the ring:* Starch present as below the ring. *Check:* Starch present in each stem in the primary xylem and in the medullary rays in all parts corresponding to those tested in the ringed stems. *May 16*, all starch had disappeared from check stems as well as from the ringed ones.
2...	20	35	
3...	10	80	
4...	15	90	
5...	12	90	
6...	15	55	
Ave.	13.7	67.5	

Ringed at base of first year's growth.

	Growth in Mm. by May 11		Growth in Mm. by May 24		Notes
	Ringed Branch	Corresponding Branch Not Ringed	Ringed Branch	Corresponding Branch Not Ringed	
1...	45	80	65	205	*May 11*, no. 4 and its corresponding check were cut and tested for starch. *Above ring:* No trace of starch in any part. *Below ring:* Starch present in primary xylem and in medullary rays. *Within ring:* Starch in primary xylem and in medullary rays. *Check:* Starch in primary xylem and in medullary rays in all regions corresponding to those tested in the ringed stems.
2...	45	80	75	180	
3...	50	80	85	210	
4...	45	90	—	—	
5...	35	55	80	240	
Ave.	44.0	77.0	76.3	208.8	

The sugar maple is commonly cited as an example of a tree that transfers its carbohydrates upward through the xylem. The trees were bleeding freely at the time the ringing was done, yet practically no translocation of carbohydrates occurred longitudinally through the xylem.

Very similar results were obtained with the pear, *Pyrus communis*, and the beech, *Fagus grandifolia*. In both, the nearer the ring was to the tip, the less was the growth and the sooner did the starch disappear above the ring. The measurements for the beech are given in table 11 and a photograph of series no. 2 in figure 3.

TABLE 11. *Fagus grandifolia. April 7 to May 24*

X. Check twigs not ringed.
B. Ringed in the middle of the one-year-old wood.
C. Ringed at the base of the one-year-old wood.
D. Ringed in the wood three to five years old which in all cases was under one centimeter in diameter.

All having the same number were fairly well matched at the time of ringing.

	X		*B*		*C*		*D*	
	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves.	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves
1.......	100	5	10	4	20	5	30	5
2.......	130	5	35	4	50	5	30	4
3.......	365	9	50	5	110	7	—	—
4.......	170	6	10	0	17	0	60	6
5.......	240	8	15	0	—	—	100	6
6.......	155	7	15	0	30	0	20	4
7.......	145	6	15	2	30	3	115	5
Ave....	186.4	6.6	21.4	2.1	42.8	3.3	59.1	5.0

One of Hartig's chief arguments that carbohydrates move upward through the xylem was based on the fact that, if a tree was ringed, the starch below the ring disappeared. He assumed that it moved upward, but there is no reason why it could not have been moved radially and used in cambial growth, or moved downward through the phloem to the growing roots. To test this latter possibility, experiments were tried with *Ostrya virginiana*

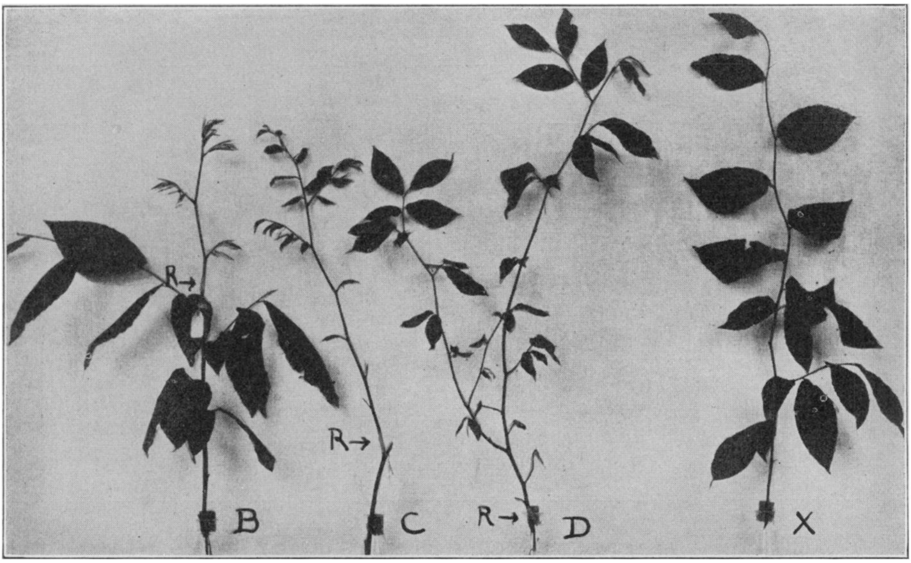

FIG. 3. *Fagus grandiflora* ringed, while dormant, at different distances from the tip. The point of ringing is indicated by *R*.

Koch, *Crataegus* sp., *Acer saccharum* Marsh., and *Fagus grandifolia* Ehrh., in which two rings were made on the same stem some distance apart.

Stems of Ostrya were ringed April 6. By May 6 growth had started and the shoots of the ringed and unringed stems were apparently of the same length, measuring for the most part about 15 to 20 millimeters. The shoots of the ringed stem, however, had used up most of their reserve food, for very little further growth took place while the shoots of the check stem continued to grow. On May 19 two of these stems were cut and tested for starch. For the stem shown in the photograph (fig. 4) the tests were as follows:

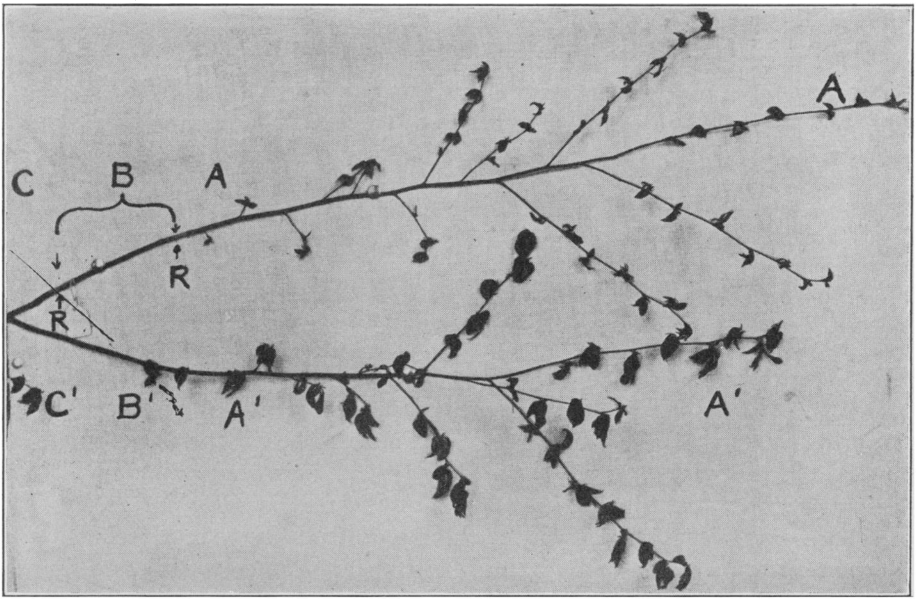

FIG. 4. *Ostrya virginiana* ringed April 6 at *RR*. Cut May 19 and tested for starch with iodine.

Ringed. *A*. Above upper ring. No trace of starch in any part either in the young twigs or in the older stem.
B. Between rings. Starch very abundant in pith, medullary rays, cortex and phloem parenchyma.
C. Below lower ring. Traces of starch in the pith cells. (See page 116 for results as to upper, middle, and lower parts of upper ring.)

Not ringed. *A*. Traces of starch in pith cells.
B. Traces of starch in pith cells.
C. Traces of starch in pith cells.

Above the upper ring: No trace of starch was present in any part, either in the young twigs or in the older stem.

Between the two rings: Starch was very abundant in the pith, medullary rays, and cortex.

Below the lower ring: There were traces of starch in the pith.

Upper part of upper ring: There was no trace of starch.

Middle part of upper ring: There were traces of starch in the pith and in some of the medullary ray cells.

Lower part of upper ring: Starch was abundant in pith and medullary rays, similar to that between rings.

Check: There were traces of starch in the pith cells in the regions corresponding to those listed above.

In the other stem tested at the same time the results were practically the same. There was more starch in the check, however, which showed very distinct traces in the pith and very slight traces in the medullary rays and cortex. In both stems the results were striking. When the sections stained with iodine were held against white paper and observed from across the room, the sections from between rings appeared almost black and the others practically colorless. These results indicate that there is practically no longitudinal transfer of carbohydrates through the xylem.

A similar experiment in double ringing was performed with several species of Crataegus. Stems were ringed April 6 and examined May 17. All showed results similar to those obtained with Ostrya; that is, in all cases starch had disappeared above the upper ring, was abundant between the rings, and was present in moderate amounts below the lower ring and in the check stems. Between the rings, starch was very abundant in the primary xylem and medullary rays; but the results were not as striking as those obtained with Ostrya, for the stem at no time contained as much starch in the pith and therefore did not appear as dark when stained with iodine.

A number of stems of *Acer saccharum* ranging in diameter from 4.5 mm. to 24.3 mm. were double-ringed on April 6 and 7. The distances between the rings ranged from 15 cm. to 107 cm. At the time of ringing most of the stems were bleeding freely. A number of the stems were cut between May 6 and May 19. In all cases starch was completely or almost completely absent above the upper ring, very abundant between rings and nearly absent to fairly abundant below the lower ring, depending on the time of cutting and the position on the tree. The data obtained from one such stem are recorded below and in table 12. This branch showed 15 annual rings at the lower ring; it was 24.5 mm. in diameter at this point, which was situated 16 cm. from the main trunk. At the level of the second ring, which was 107 cm. from the first, the diameter of the branch was 20.2 mm. The check branch was not perfectly matched but was somewhat smaller than the ringed one. The diameter at its base was 22.3 mm.

Above the upper ring: There was no starch in any part except in a few scattering cells of the primary xylem.

Between the two rings: Starch was very abundant in the primary xylem and the medullary rays.

Below the lower ring: Starch was fairly abundant in the primary xylem and in the inner part of the medullary rays. The medullary rays of the outer annual ring were emptied of starch, those of the second contained only traces, those of the third still larger amounts, while in the fourth annual ring the starch was abundant.

Check: At the base starch was fairly abundant in the primary xylem and in the medullary rays of the inner annual rings, disappearing in the third ring and entirely absent in the outer two. Farther out on the stem, at a point corresponding to that of the upper ring on the ringed branch, the diameter was 20.5 mm. At this point starch was mostly absent from the outer nine rings but was fairly abundant in the inner four. Still farther out, where the diameter was 12 mm., starch was present in distinct quantities in the primary xylem only.

The stems were cut in pieces 12 cm. long, which were then peeled to the cambium. These pieces of xylem were centrifuged and the small amount of sap obtained was hydrolyzed with hydrochloric acid and tested for reducing sugar. Samples corresponding to 1 cc. amounts from the stems immediately above the upper ring and between the rings were tested. From above the ring 0.3 mg. of cuprous oxide was obtained on boiling with Fehling's solution, while 2.0 mg. were obtained from between the rings. A second test was lost by accident, but at the time of filtering through the asbestos there was a very distinct precipitate of the cuprous oxide from the sample between the rings and but a very faint trace of the oxide from the other sample. Another accident resulted in the loss of the remainder of the sap, so no further tests could be made.

Samples of the oven-dried wood were sawed into 5 mm. lengths and extracted in 250 cc. of 80 percent alcohol for 72 hours at 37° C. After driving off the alcohol and hydrolyzing with hydrochloric acid by heating to 76°, quantitative tests were made for reducing sugar as shown in table 12.

TABLE 12. *Acer saccharum. Sugars from xylem soluble in 80% alcohol. Hydrolyzed extract made up to 100 cc. 30 cc. samples tested from between rings and above, 25 cc. samples from the others*

	Dry Weight of Xylem Extracted	Individual Determinations Expressed as Mg. Invert Sugar			Average of Determinations	Mg. Invert Sugar Calculated for 25 Gms. Dry Wood
Above upper ring....	23.33	14.15	14.66	14.58	14.46	53.91
Between rings.......	31.78	59.6	59.85	59.05	59.5	155.84
Below lower ring.....	44.10	55.55	54.38	—	54.965	124.65
Check..............	37.07	40.08	39.10	—	39.59	106.80

From the data shown in table 12 it is evident that the removal of soluble carbohydrates from between two rings does not occur or is very much retarded. The carbohydrates above the upper ring were very much reduced. It is probable that, if a smaller stem had been ringed, the sugar content above the ring would have been very much less; for in such cases shoot growth is quickly checked while in the present instance the shoot growth was apparently no less than in the check. The sugar content below the lower ring was less than that between the rings, showing that from this region some of the carbohydrates had been carried backward to the trunk whence they were carried towards the roots or to branches higher up. The unringed branch showed a sugar content higher than that above the ring and lower than that between upper rings, or below the lower ring, as would be expected.

After the removal of the soluble carbohydrates the residue was treated according to the Sachs method to determine the starch content. The material was boiled for two and one half hours under a reflux condenser in a flask with 10 percent hydrochloric acid of 1.9 specific gravity. The data obtained are recorded in table 13.

TABLE 13. *Acer saccharum. Polysaccharides from xylem hydrolyzed by Sachs method. Extracts made up to 500 cc., 25 cc. of this diluted to 200 cc. and 50 cc. samples analyzed*

	Dry Weight of Xylem	Mg. of Sugar Expressed as Glucose		Average of Determinations	Mg. of Glucose per 25 Gms. Dry Wood
Above upper ring	23.33	49.88	49.02	49.45	4,429
Between rings	31.78	73.00	72.55	72.775	4,580

The data indicate that there are more polysaccharides present in the stem between the rings than above, an equivalent of 151 milligrams of glucose. It is very evident, however, that by this method of extraction much material of the wood that is not starch is hydrolyzed. The iodine test showed only very faint traces of starch above the rings, yet by this method it would seem that this part of the stem contained starch to the extent of about 17.1 percent of the dry weight. It is very probable that pentosanes and possibly other polysaccharides were hydrolyzed.

TABLE 14. *Acer saccharum. Sugars from wood soluble in 95% alcohol. Extract made up to 100 cc., 25 cc. samples taken*

	Determinations Expressed as Mg. of Invert Sugar		Average of Determinations	Total Mg. Soluble Sugar Calculated for 25 Gm. Dry Matter
Above upper ring	12.1	11.8	11.45	45.80
Between rings	31.35	31.35	31.35	125.40

A second set of samples was extracted after a somewhat different manner. Pieces of xylem were sawed more finely into sections about one millimeter thick. Twenty-five gram samples of this dry material, including the sawdust produced in the process, were placed in 250 cc. of 95 percent alcohol and boiled for three hours in a flask with a reflux condenser. The solution was filtered off and the residue was extracted in the same way in fresh alcohol for a second three hours. The filtrate was then freed of alcohol, hydrolyzed with 10 percent hydrochloric acid for three minutes and tested for reducing sugar. The results are recorded in table 14.

Evidently somewhat less sugar was extracted in this way than was extracted in 80 percent alcohol. The ratio of the sugar content between rings to that above, however, is nearly the same in both determinations. These are respectively 2.74 to 1 and 2.89 to 1. The alcohol was removed from the residue by heating under vacuum. Water (300 cc.) was added and the whole was heated to 80°, cooled, and 0.2 gms. taka diastase added. At the time the diastase was added, the filtrate from the wood between rings showed a distinct blue with iodine while the other showed none. After standing 12 hours with taka diastase, 50 cc. samples of each were taken, hydrolyzed 3 minutes with 10 percent HCl and tested for reducing sugar. Calculated as glucose, the sample from between the rings contained 68.05 mg. of sugar and that from above the rings 26.24 mg. The total volumes of solutions were not exactly equal, so that these samples are not strictly comparable. The remainder of the solution was boiled for 3 minutes with 10 percent HCl in contact with the residue. The solution was filtered off, neutralized, and tested for reducing sugar. This is expressed in table 15 as glucose, but it is probable that some maltose remains.

TABLE 15. *Acer saccharum. Sugar obtained from residue by treatment with diastase and acid after removal of sugars soluble in 95% alcohol. Extract made up to 500 cc., 50 cc. samples taken*

	Individual Determinations		Average	Total in 500 cc.	Removed Before Treatment of Residue with Acid	Total for 25 Gms. Dry Wood Expressed as Glucose
Above rings	51.9	51.95	51.925	207.70	26.24	233.94
Between rings	92.25	93.08	92.665	370.66	68.50	439.16

A number of stems of *Fagus grandiflora* were double-ringed and results very similar to those described for Acer were obtained. All the stems tested with iodine showed a large amount of starch between rings and little or no starch above the upper ring. One experiment for which sugar analyses were made will be reported in detail. A young sapling was ringed 10 cm. from the ground and a second ring was made 70 cm. above the first. At this point the diameter of the stem was 30 mm. The rings were about 3 cm. broad. The ringing was done April 7, and the tree, with the check standing within three feet of it, was cut May 27. At this time the shoots had evidently completed their growth, but there was no apparent difference in the growth of the new shoots.

The tests for starch were as follows:

Above upper ring: No starch was present except in a very few scattered pith cells.

Between rings: Starch was very abundant in medullary rays and pith.

Below lower ring: There were distinct traces of starch in the medullary rays and in a few pith cells.

Lower part of upper ring appeared the same as between rings.

Upper part of upper ring: Starch was fairly abundant but distinctly less abundant than in the lower part.

Lower part of lower ring: Starch was fairly abundant in medullary rays and pith but less in the latter than between the rings.

Upper part of lower ring: The starch content was the same as between the rings.

Check: Traces of starch were present in smaller medullary rays and in the pith but less than just below the lower ring. This was true for all parts corresponding to those tested as described above.

The stems were cut into pieces 12 cm. long, from which all tissues outside the cambium were removed. These pieces were centrifuged, and the sap was tested for invert sugar after hydrolyzing with hydrochloric acid. The exact amount of sap remaining after removing 4 cc. samples was not determined as the tubes were rinsed out with water.

TABLE 16. *Fagus grandiflora. Sugar obtained from centrifuged stems*

	Green Weight of Sticks	Mg. Invert Sugar in 4 Cc. Samples	Mg. Invert Sugar in Remaining Sap	Total Invert Sugar Obtained.	Total Mg. Invert Sugar from Centrifuged Sap per 100 Gms. of Xylem
Check	125.0	2.03	1.08	3.11	2.49
Above ring	185.4	1.25	0.72	1.97	1.06
Between rings	219.6	1.67	3.76	5.43	2.47

The amounts of sap obtained were so small that the analyses cannot be fully depended upon, yet there seems to be clear indication that more sugar is present in the sap centrifuged from the xylem between the rings than from that above.

TABLE 17. *Fagus grandiflora. Sugar soluble in 80% alcohol hydrolyzed and expressed as invert sugar*

	Mg. Invert Sugar in 25 Cc. Samples		Average	Total Mg. Invert Sugar in the 50 Gms. Dry Wood
Check	42.34	43.7	43.02	344.16
Above rings	42.30	41.35	41.825	334.60
Between rings	61.08	60.20	60.64	485.12

The wood was sawed into short sections about a millimeter in length. After drying in the oven, lots of fifty grams each of this material, including the sawdust, were extracted in 250 cc. of 80 percent alcohol at 37° for 24 hours, and again in fresh alcohol for 72 hours. After heating to 80° the solution was filtered off, the alcohol was removed by repeated evaporation, and the solution was finally boiled for 3 minutes with 10 percent hydrochloric acid, neutralized, and made up to 200 cc. The amounts of sugar found are shown in table 17.

The residues were shaken up with 250 cc. of water and 0.2 gm. taka diastase. After 12 hours the sawdust still contained abundant starch. The material was then placed in a steam autoclave at 15 pounds pressure for 45 minutes. Two-cubic-centimeter samples diluted with 5 cc. of water and tested with iodine showed deep blue in the sample from between the rings and very faint traces of blue in those from the check and from above the rings. Five tenths of a gram of diastase was added to each and left 18 hours, but on examination starch was still present in the sawdust and in the small sections of wood. The material was then autoclaved a second time at 15 pounds for 10 minutes. On testing the extract as before, only that from between the rings clearly showed the presence of starch.

Without attempting to extract more of the starch, the solutions were filtered off and digested with 0.25 gm. of taka diastase. Each of the extracts was then made up to 500 cc. and 25 cc. samples were tested for sugar. This is expressed in the table as maltose, but it is very probable that much of it was really glucose. Relative values, however, are all that are necessary.

TABLE 18. *Fagus grandiflora. Sugar obtained from residue by heating under pressure and digesting with diastase*

	Single Determinations Expressed as Maltose		Average	Total Sugar Present in 50 Gms. Dry Wood Expressed as Maltose
Check	46.03	40.24	43.14	862.80
Above rings	51.46	52.46	51.965	1039.30
Between rings	89.25	89.78	89.52	1790.40

DISCUSSION

The experiments with ringing accompanied by removal and non-removal of leaves clearly show that some substance necessary for growth passes upward through the phloem and that, if the leaves remain above a ring, they are able to supply some of this substance. This substance may function as a food, supplying building material and energy, or it may function merely as an osmotically active agent, thereby enabling the tissue to compete successfully for water, or, as is more probable, it may function in both rôles. Analyses show that ringing when leaves are removed results in a decrease both of osmotic pressure and of sugar content. Removal of leaves without ringing also decreases the osmotic pressure and the sugar content below those of the normal stem with leaves. The data obtained are not sufficient to enable one to determine with any degree of assurance whether sugar is the only or even the chief substance concerned.

The experiments with ringing dormant stems indicate that the growth above a ring practically ceases when the carbohydrates in this region have disappeared. Even the starch of the xylem itself is not digested and removed upward unless a path through the phloem is open. If that part above the ring is so short that the bud merely elongates but does not open its leaves, growth ceases completely, and later the enlarged bud or partially opened leaves wither and die. If sufficient food was above the ring to enable one or two leaves to open, growth often slowly recommences, probably because of the food made available by the new leaves.

The experiments with double ringing show even more clearly that the xylem does not serve as a tissue for longitudinal translocation of the carbohydrates stored in it, for between rings the content both of starch and of soluble sugars is much higher than either above or below the part thus isolated. It would seem that the removal of carbohydrates from the xylem occurs only radially through the medullary rays and that longitudinal transfer in either direction is through the phloem only. In a ring 1 cm. wide starch was still present when all the starch had disappeared immediately above the ring. Later, however, the upper part had become depleted while the lower part was still full. Diffusion may have accounted largely for the movement through this short distance. Observation on this point has not been made, but it seems probable that much of the food from between rings will be eventually used up in cambial growth.

As was previously stated, Atkins (1916), finding appreciable quantities of sugars in the sap centrifuged from the stems of various woody plants, concluded that these must move upward with the "transpiration stream" and that one of the principal functions of the xylem is to transfer these sugars. The data here recorded, however, show that no appreciable amounts of sugar are transferred vertically through the xylem. In the experiments in which the leaves were removed above a ring, it seems possible that the lack of rapid transpiration might partly account for the failure of the xylem to transfer food; however, in the experiments in which dormant wood was ringed some distance from the tip plenty of leaves were produced above the ring to carry on rapid transpiration, yet this seemed to have no effect in causing the removal of either starch or soluble sugar below the ring, or from between rings in those stems that were double-ringed. In the the maple reported in tables 12–15, and in the beech reported in tables 16–18, there was a very large leaf surface that must have required quantities of water, but even the soluble sugars were not removed from between rings.

It will be necessary to make further tests on centrifuging the xylem before definite conclusions can be safely drawn, but the little that has been done at least suggests that even the sugar in the vessels does not normally move with the water in transpiration. We know that when a tree, such as the maple, is tapped, sugar solution will flow through the vessels. This is not proof, however, that in an uninjured tree there is any flow of solution through the vessels. If this were true, one would expect a depletion of carbohydrates below a ring in the maple, especially when it is ringed during the season of sap flow and when the ring is only one to two centimeters broad.

A possible frequent interposition of living cells across conducting tubes may readily prevent a flow of solution, and the water may normally move largely by diffusion. When a tissue is cut, however, as in pruning or in tapping, there is probably an actual flow of solution through the opened vessels which might also result in a depletion of storage materials from adjacent tissues. The movement of water through uninjured xylem may occur chiefly by diffusion as in the case of the entrance of water from the soil into a root. In the latter case there is certainly no flow of solution, as the amount of water taken up has no relation to the amount of solutes absorbed. Data reported by Kiesselbach (1916), who grew plants in soil, indicate that increased transpiration does not increase ash absorption. Experiments by the writer in collaboration with Dr. E. Artschwager and Dr. N. B. Mendiola, that are nearly ready for publication, show that doubling the transpiration from plants growing with their roots in nutrient solutions has no tendency to increase salt absorption.

It may even be that at least some of the mineral nutrients move primarily through the phloem. It is true that, if a stem is placed in a solution of dye, the dye will rise rapidly through the xylem, but whether it will do so in a normally rooted plant has not been conclusively proven. The writer has found, however, that lithium chloride applied to a rooted plant will move through the xylem past a ring. It is possible, however, that it was not carried in the "transpiration stream" but rather that it moved past the ring by diffusion. Lithium salts will diffuse much more rapidly than sugars, and cell membranes seem to be very permeable to them. The lithium was found in the phloem and cortex above the ring as well as in the xylem.

A number of papers have been published in which it has been shown that certain dyes or salts appear to travel in the "transpiration stream" through the xylem when the roots of the plant are placed in the solutions. But in many cases the dyes or salts used may have had toxic effects as a result of which the cells that might normally retard their movement may have been killed or their permeability may have been increased. Furthermore, it has been found in a number of instances that the solutes appeared to travel at about the same rate in the phloem region as in the xylem. Bokorny (1890) found that, when roots were placed in solutions of iron sulphate or of various dyes and the leaves were exposed to very drying conditions, the solutes were found in the phloem region at about the same height as in the xylem region. When on the other hand a cut stem was placed in the solution, the movement through the xylem was distinctly the more rapid. Because he always found the solutes not in the lumina but in the walls of the thicker-walled elements, such as the vessels, sclerenchyma, and collenchyma cells, Bokorny came to the conclusion, which has since been clearly disproved, that water moves through the walls by imbibition. Though his conclusions are of little value, his data at least suggest that solutes are not necessarily carried by the "transpiration stream."

It will be necessary to conduct experiments using rooted plants and various non-toxic salt solutions before any very definite conclusions can be drawn as to the region of transfer of salts in plants.

SUMMARY

Defoliated stems from which a ring of tissue extending to the cambium is removed cease to continue growth.

This cessation is due to the inability of the xylem to carry the necessary food.

This food is needed not only to supply energy and building material but also to increase the osmotic concentration of the tissues, thereby enabling them to absorb water.

This food consists, at least partially, of carbohydrates.

If the stem above a ring is not defoliated, the leaves are able to supply sufficient of this food to allow for considerable growth.

When dormant stems are ringed, the growth above the rings ceases soon after the starch supply is depleted, and the greater the supply of starch above a ring the longer will growth continue.

The carbohydrates stored in the xylem below the ring can not be removed through the xylem but must be transferred radially to the phloem, where they may be carried downward if there is no second ring below.

The carbohydrates of the xylem between two rings remain there at least for some time after those above the upper ring and those below the lower ring have been mostly removed.

Although large amounts of carbohydrates are stored in xylem tissues, there is no appreciable longitudinal transfer of sugars through these tissues.

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